thin flippers that flap like a bird wing to produce thrust underwater, and are used to support the trunk on land. Phocid forelimbs function solely in steering while underwater but are usually held flush with the body wall, and are not a significant source of propulsion. On land, most phocids do not use their forelimbs as a weight-bearing appendage.

p3030 Walrus (*Odobenus*) flippers are short compared to other pinnipeds, but are very broad and have tiny nails on the dorsal surface. Otariids have elongate and thin flippers with a slight crescent of skin at the ends of each digit. Phocid flippers are divided between some of the digits, and long thin nails extend beyond the dorsal surface of all five digits.

p3040 The digits of pinnipeds also have unique characteristics (Howell, 1930). All pinnipeds have elongated the digits by developing bars of cartilage at the ends of each digit. These cartilaginous extensions are longest in otariids, slightly shorter in the walrus and shortest in some phocids. Metacarpal I is longer and thicker than metacarpal II in all pinnipeds except phocines.

F

p3050 Pinnipeds also display large and complex forelimb muscles. The walrus has large and powerful muscles, with relatively the same sized muscle bellies as otariids.

p3060 Otariid isolate more than half of the forelimb musculature in the proximal portion of the forelimb. The triceps muscle complex is relatively large, and allows for elbow retraction. Muscles acting on the otariids wrist create palmar flexion, which is the main source of propulsion. Otariids also have muscles acting on the digits: interossei, digital abductors and adductors, and in some specimens a single lumbrical. Phocids have an enlarged triceps muscle complex.

p3070 The earliest fossil pinniped, *Enaliarctos mealsi*, already had forelimbs modified as flippers. No fossils indicate the transition between terrestrial carnivores and aquatic pinnipeds (Berta *et al*., 1989).

B. Sea Otters

s0870

p3080 Sea otters (*Enhydra*) do not use their forelimbs while swimming. The forelimbs are specialized in movements requiring great dexterity: prey manipulation, grooming, and caring for young (Howard, 1973).

p3090 Sea otter forelimbs are small and retractable claws extend from each of the digits. The digits cannot act individually as they are connected by soft tissue webbing. Thick pads line the palmar surfaces of digits. Forelimb musculature is well developed.

p3100 The giant extinct sea otter *Enhydritherium* was propelled by its forelimbs, but all modern sea otters are pelvic paddlers with enlarged hindlimbs.

C. Polar Bears

s0880

p3110 Polar bears are powerful swimmers but also walk on ice or land. The forelimbs are incredibly strong and are the main sources of propulsion while swimming, killing prey, fighting, and hauling out of the water. Alternating strokes of forelimb flexion generate propulsion while swimming and the hindlimbs trail and remain motionless. While fighting another, polar bears will stand on their hind limbs, wrap forelimbs around another and bite. To haul out of the water, the polar bear pulls itself mostly out of the water with its stong forelimbs, and uses the hindlimbs after most of the body mass is out of the water. While walking on ice or land, polar bears place the whole hand flat on the substrate.

p3120 Polar bear forelimbs are similar to other bears, except that the scapula is widened by a postscapular fossa. This wider fossa increases the area of origin for the subscapularis muscle. The subscapularis may play an important role in swimming.

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s0890

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Forensic Genetics

c0120

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I. Introduction

s0910

p3150 Molecular genetics provide a powerful tool for the conservation and management of cetaceans and other marine mammals-the identification of products derived from hunting, strandings, and fisheries bycatch (Baker and Palumbi, 1994; Cipriano and Palumbi, 1999; Dalebout *et al.*, 2002a). Such products include soft tissue such as meat, organs, blubber, skin, and blood, as well as teeth, bone, baleen, and hair. The examples given here are for cetaceans, but the approaches can be applied to carnivores and sirenians. Although the species origins of these products may be

impossible to determine on the basis of appearance, they contain DNA that can be amplified, sequenced, and compared to sequences from known specimens. With advances in molecular methods over the last decade, DNA can now be recovered from almost any biological source, even products that have been preserved, cooked, or canned (Asensio Gil, 2007). With a comprehensive reference library of homologous sequences, such as the control region or cytochrome *b* gene of the mitochondrial (mt) DNA, a product of unknown origin can be attributed in most cases to one of the approximately 90 accepted or proposed species of cetaceans (Baker *et al.*, 2003). If a comprehensive archive of tissue is maintained as part of a regulated hunt or documented fisheries bycatch, it is also possible to trace the origins of a product to a specific individual by matching of nuclear AQ48 DNA genotypes (Cipriano and Palumbi, 1999; Dalebout *et al.*, 2002; Palsbøll *et al.*, 2006). Although many of the applications of these methods are not intended for criminal prosecution, they share the common methodology of wildlife forensic genetics (US Fish and Wildlife Service, 2001) and the broader objectives of improving controls over trade and exploitation of protected species.

p3160 The forensic use of molecular genetic methods is of particular interest to the International Whaling Commission (IWC), as it attempts to develop a Revised Management Scheme (RMS) for the regulation of any future commercial whaling, and to the Conventional on International Trade in Endangered Species of Wild Fauna and Flora (CITES), as it attempts to implement a verifiable system for controlling trade in cetacean products. An important application of forensic genetics has been to identify the species and, in some cases, geographic origins of whale, dolphin, and porpoise products AQ49 sold in two countries with active commercial markets: Japan and the Republic of (South) Korea (Baker and Palumbi, 1994; Baker *et al.*, 1996; Grohman *et al.*, 1999; Simmonds *et al.*, 2002). Of particular, concern has been the sale of protected species or populations (stocks) derived from illegal, unreported, and unregulated (IUU) exploitation (Baker *et al.*, 2000b, c; Baker *et al.*, 2002). Other applications include identifying stranded individuals and fisheries bycatch, particularly for poorly described species such as beaked whales (Henshaw *et al.*, 1997; Dalebout *et al.*, 1998; Dalebout *et al.*, 2004), and monitoring of trade in pinniped penises sold as aphrodisiacs (Malik *et al.*, 1997). Most recently, molecular identification of species and capture–recapture analysis of DNA genotyping from individual products have been used to estimate the true level of bycatch for some species sold in commercial markets (Baker *et al.*, 2006; Baker *et al.*, 2007).

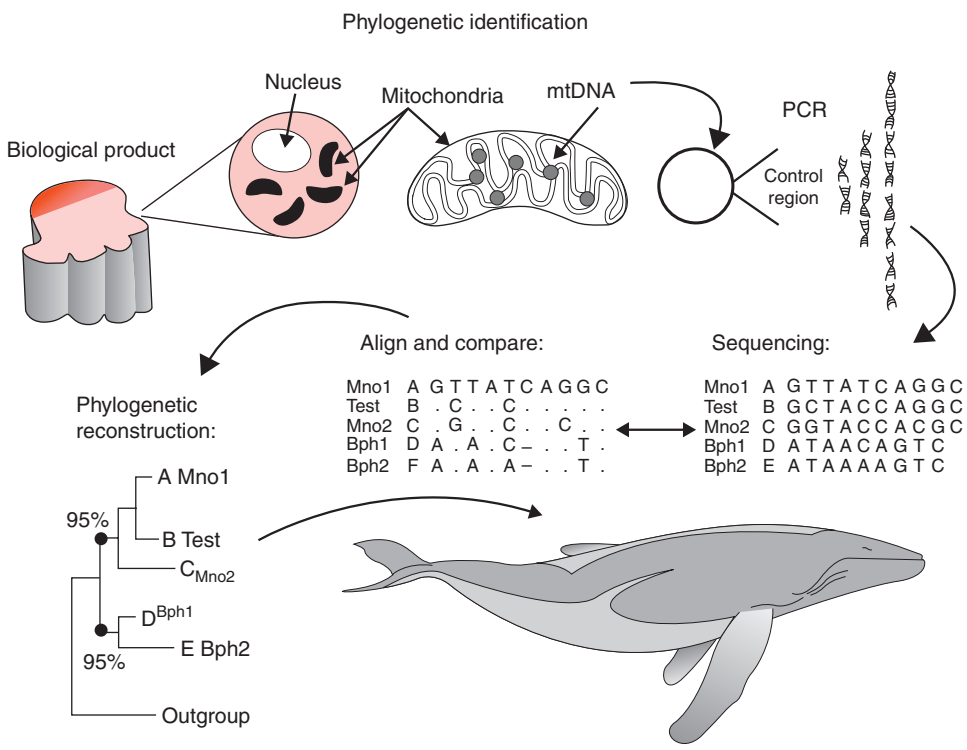
s0920 II. Molecular Taxonomy and Identification of Cetacean Species

p3170 The methods for molecular identification of species in trade developed initially from basic research on species-level phylogenetic relationships and the genetic structure of populations (Baker and Palumbi, AQ50 1994 ; Baker *et al.*, 1996, 1994; DeSalle and Birstein, 1996; Malik *et al.*, 1997; Roman and Bowen, 2000; Shivji *et al.*, 2002). More recently, there has been an explosion of interest in the systematic application of these techniques to basic organismal taxonomy (Hebert *et al.*, 2003; Tautz *et al.*, 2003; Blaxter, 2004), including cetaceans (Baker *et al.*, 2003; Ross *et al.*, 2003; Dalebout *et al.*, 2004). Now referred to as "molecular taxonomy" or "DNA taxonomy," the objective of identifying known species from a designated homologous gene sequence differs from the usual goal of molecular phylogenetics, which is more concerned with hierarchical relationships above the species level. For species identification of cetaceans and other animal species, the molecular marker of choice has usually been mitochondrial DNA (mtDNA). In general, mtDNA offers two important advantages over nuclear genetic markers. First, because of its maternal inheritance and absence of recombination, the phylogenetic relationship of mtDNA sequences reflects the history of maternal lineages within a population or species. (If hybridization is encountered, nuclear markers are required to identify the paternal species; discussed later). Second, all else being equal, the effective population size of mtDNA genomes is one-fourth that of autosomal nuclear genes and its rate of random genetic drift is proportionately greater. This results in more rapid differentiation of mtDNA lineages among populations, compared to nuclear genes, and consequently greater sensitivity in the detection of recent historical demographic or speciation events. The ability to detect population differentiation is also be enhanced by the rapid pace of mtDNA evolution, which is generally estimated to be five to ten times faster than nuclear coding DNA in most species of mammals.

p3180 Although one approach to molecular taxonomy has advocated a universal "DNA barcode of life" for all animal species based on the mtDNA cytochrome *c* oxidase I gene (COI) (Hebert *et al.*, 2003), it is not clear that this locus is the most sensitive or reliable for identification of cetaceans (Amaral *et al.*, 2007). Instead, species-level identification of marine mammals has relied primarily on the phylogenetic reconstruction of sequences from the mtDNA control region (sometimes referred to as the D-loop) or the cytochrome *b* gene. The control region of the mtDNA does not code for a protein or RNA and, in the absence of these constraints, accumulates mutational substitutions more rapidly than other regions. For this reason, it has become the marker of choice for most studies of the population structure of cetaceans and pinnipeds. The cytochrome *b* gene, a protein region of the mtDNA, has also been used widely for species-level phylogenetics (Arnason and Gullberg, 1996; LeDuc *et al.*, 1999) and in some cases, for population structure of marine mammals (Lento *et al.*, 1997). Because of the large number of reference sequences available on public databases such as *GenBank* and *EMBL*, both loci have been used for species-level identification of marine mammals.

p3190 The basic steps involved in the phylogenetic identification of an unknown specimen or market product are illustrated in Fig. 1. First, mtDNA is extracted from the product in question, such as a flensed piece of skin and blubber from a commercial market. Second, a fragment of the mtDNA control region is amplified from the product via PCR (Saiki *et al.*, 1988)—a cyclic, *in vitro* enzymatic reaction that results in the exponential replication of a small targeted fragment of mtDNA (usually <1000 base pairs). Third, the exact nucleotide sequence of the amplified fragment is determined using a dideoxy-terminator sequencing reaction, followed by electrophoresis through an acrylamide gel. In most laboratories, this step is now automated with a computer-assisted laser scanner. Fourth, the sequence of the product, now referred to as the "test sequence," is aligned to and compared with the sequences from reference samples. For protein coding regions, such as cytochrome *b* or COI, alignment is unambiguous among cetaceans (or other mammals) because of the absence of insertions or deletions (indels) in the codon sequences. For the noncoding CR, however, the presence of numerous single- and multiple-base indels often requires an automated alignment procedure and manual confirmation to optimize identification.

p3200 Finally, the "test sequence" is grouped with the most closely related reference sequences in the reference database using phylogenetic reconstruction methods, such as minimum evolution (neighbor joining), maximum parsimony, or maximum likelihood. The reconstruction is usually represented as a "tree," with closely related sequences forming neighboring branches. This approach allows a hierarchical



f0300 **Figure 1** *The basic steps involved in species identification of an unknown cetacean product using of nucleotide sequences amplified, by PCR, from the mtDNA control region. The "test sequence" derived from an unknown species origin is aligned and compared to a comprehensive reference database of sequences from specimens of known provenance, such as that available on the web-based program, www.DNA-surveillance.*

comparison to establish first the suborder and family derivation using a small number of reference sequences from each of a large number of species. Once the family or subfamily is established, the phylogenetic reconstruction of the test sequence can be repeated using a larger number of reference sequences to better represent the diversity within each of the smaller number of species at this taxonomic level. A close relationship or match with a "reference" sequence provides evidence for identification of the species origin of the product. One or more "out-groups" (i.e., distantly related species) are used to protect against a misclassification error. The strength of support for an identification or phylogenetic grouping is evaluated by "bootstrap" resampling of the sequence data. The relative support for a grouping or branch in the tree is shown as the percentage agreement from a large number (>1000) of bootstrap simulations.

p3210 As a conservative approach to forensic identification, a species identification should be considered "confirmed" only if the test sequence is "nested" within the range of reference sequences for a given species. This is necessary because the molecular systematics of some marine mammals, particularly the cetaceans, are not fully described (Reeves *et al.*, 2004; discussed later). If a test sequence is intermediate between two groups of reference sequences, rather than nested within one or the other, it could be a related species or subspecies not included in the reference database. Where a reference database is considered to be comprehensive in regards to known species, the finding of a particularly divergent sequence could be evidence of an unknown or unrecognized species or subspecies (Baker *et al.*, 1996; Dalebout *et al.*, 2004; Dalebout *et al.*, 2007).

p3220 When a large set of reference sequences is available from the range of a single species, it is possible to use intraspecific variation to evaluate the geographic origin of a sample (Baker *et al.*, 2000a). In many cases, the management of marine mammals is based on geographic populations or stocks (Dizon *et al.*, 1992). Catch quotas and limits of incidental mortality from fisheries bycatch are usually set according to such stock definitions, as well as according to species. Hunting may be allowed in an abundant stock but prohibited in another stock of the same species that is depleted from past exploitation. However, the ability to identify or estimate the geographic origin of a specimen or product is determined by the genetic distinctiveness of the recognized stocks, as well as by the comprehensiveness of the reference samples.

III. Web-Based Species Identification with www.DNA-surveillance

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p3230 To assist in the genetic identification of whales, dolphins, and porpoises, an interactive application for phylogenetic identification has been developed and is accessible through the website, http://www.DNA-surveillance (Ross *et al.*, 2003). *DNA Surveillance* (2008) implements phylogenetic methods for identification of species within a particular taxonomic group, such as the currently available datasets for whales, dolphins, and porpoises. The application automates the procedure of species identification by aligning a user-submitted gene sequence of unknown origin against a set of validated reference sequences. The evolutionary distances between the unknown

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or "test" sequence and each of the reference sequences is computed and a phylogenetic tree displays the affinity of the unknown sequence to the reference sequences.

p3240 *DNA Surveillance* differs in several important ways from the blast search options available on the website of the international genetic database, GenBank (Ross and Murugan, 2006). The problems associated with using GenBank for species identification are particularly relevant to cetaceans, where the primary taxonomic identification of the voucher specimen can be ambiguous or incorrect (Henshaw *et al.*, 1997; Dalebout *et al.*, 1998). Sequences entered in GenBank are not curated and often are not associated with identifiable reference or voucher specimen material. The taxonomic representation of a BLAST search is difficult to judge because of the large number of redundant gene sequences for some species, the absence of sequences from other closely related species and the nature of the pair-wise alignment and search algorithm. BLAST and related search engines seek only locally maximal matches in pair-wise comparisons. The extreme (E) value associated with each sequence hit in a BLAST search is not a rigorous measure of evolutionary distance or genetic similarity, and is dependent on the size of the database being searched (Karlin and Altschul, 1990). Inconsistent application of keywords also reduces the power of searching GenBank by fields, impeding effective data mining. By contrast, *DNA Surveillance* is designed specifically for species identification of selected taxonomic groups. The reference sequences in *DNA Surveillance* are prealigned at each hierarchical level of the database, using a mixture of algorithmic and manual methods, to create an optimized alignment. The sequences in *DNA Surveillance* were chosen to reflect known phylogenetic diversity at the species and population level (where available). The genetic distances and trees in *DNA Surveillance* are calculated using standard phylogenetic algorithms, as implemented in the Phylogenetic Algorithms Library (Drummond and Strimmer, 2001).

p3250 The reference data sets mounted on *DNA-surveillance* comprise sequences from both the mtDNA control region and cytochrome *b* gene. Reference sequences were selected to reflect the generic, specific, or geographic diversity observed at a taxonomic level and to maximize the discriminatory power of the analysis. In an effort to validate the dataset, most sequences were derived from specimens that had been identified by experts and for which diagnostic skeletal material or photographic records were collected (Dizon *et al.*, 2000). Data sets are arranged hierarchically, allowing initial family-level identification of cetaceans and subsequently more detailed analysis within the suborders Mysticeti (baleen whales) and Odontoceti (toothed whales). The datasets currently mounted on *DNA-surveillance* at this writing are taxonomically comprehensive, with a total of 399 control region sequences and 264 cytochrome *b* sequences representing 88 species (DNA-surveillance, 2008). Sequences from documented specimens represent all of the 83 species recognized by Rice (Rice, 1998), with two exceptions: the Atlantic hump-backed dolphin, *Sousa teuszii*, and the Indian hump-backed dolphin *S. plumbea* (the latter of which has not been accepted by IWC). The datasets also includes one species found in an alternate species listings, *Platanista minor* (IUCN Red Book), and seven species accepted, revised, or proposed in publications since Rice (1998): *Balaenoptera omurai* (Wada *et al.*, 2003), *Eubalaena australis* and *E. japonicus* (Rosenbaum *et al.*, 2000), *Mesoplodon perrini* (Dalebout *et al.*, 2002b), *M. traversii* (van Helden *et al.*, 2002), *Orcaella heinsohni* (Beasley *et al.*, 2005), and *Sotalia guianensis* (Caballero *et al.*, 2007). Both the control region and cytochrome *b* datasets include sequences from multiple specimens for most species.

p3260 In a typical analysis, the user copies a DNA sequence (in FASTA or text format) into a data input window and chooses the appropriate reference data set. The test sequence is aligned by a simple profile alignment against the pre-aligned data set of reference sequences. The user can also choose a computationally more intensive full alignment of the test and reference sequences be performed as part of the analyses. A neighbor-joining (NJ) tree is built from the table of evolutionary distances (Saitou and Nei, 1987) and rooted using an out-group appropriate for each data set. The phylogenetic tree, in both graphic and text format, and a table of distances are displayed and can be downloaded to the user. An optional bootstrap analysis (Felsenstein,1985) can be performed to assess the robustness of the resulting phylogenetic tree.

IV. Taxonomic Uncertainties and Species Identification

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Problems in molecular identification of cetacean species can p3270 occur if taxonomic sampling is incomplete (missing species) or within-species sampling is not sufficiently representative of diversity. In cases of deep intraspecific diversity or shallow interspecific divergence, an unknown test sequence could group with the next most closely related species as a result of such sampling error. For this reason, it is important that levels of genetic diversity within, and divergence between species in a group of interest are assessed as part of the development of a molecular taxonomy (Dalebout *et al.*, 2007). As a conservative approach, Baker *et al.* (1996) suggested that identification of a test sequence should be considered conclusive only if it nests within the diversity of reference sequences for a given species. In practice, this is less crucial if phylogenetic support for the species-level grouping is strong and the taxonomic sampling is known to be complete.

p3280 More problematic are cases where the phylogenetic reconstruction of mtDNA sequences is not concordant with accepted species taxonomy described from morphological characteristics. Instead of the expected pattern of species-specific monophyly, where all mtDNA lineages (sequences) from a given species group with each other, some lineages group with another species (paraphyly) or fail to form species-specific groups (polyphyly). The reasons for species-level paraphyly or polyphyly of mtDNA are varied and include recent hybridization as well as incomplete lineage sorting due to recent speciation (Funk and Omland, 2003). If species or species complexes are truly paraphyletic, it is unlikely that a phylogenetic approach to "species" identification will be successful. Instead, molecular identification can only to be made with confidence to a higher taxonomic rank within which mtDNA lineages are monophyletic (e.g., genus or subfamily). Although species-level monophyly of mtDNA has been demonstrated for many species of cetaceans, including the beaked whales (Dalebout *et al.*, 2004; Dalebout *et al.*, 2007) and baleen whales (Baker *et al.*, 1993; Rosenbaum *et al.*, 2000; Wada *et al.*, 2003), apparent paraphyly is reported for some species of the family Delphininae, particularly the genera *Stenella*, *Tursiops*, and *Delphinus* (Dizon *et al.*, 2000; Reeves *et al.*, 2004).

V. Individual Identification and a Diagnostic "DNA Register"

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p3290 An alternative to the species identification of an unknown specimen or product is individual identification by DNA genotyping or "profiling" using variable nuclear markers. As in human forensic genetics,

a combination of variable nuclear markers (such as microsatellites, Single Nucleotide Polymorphisms (SNPs), or nuclear introns) can be used to establish individual identity with high probability (or to exclude identity with certainty, barring experimental error). The DNA profile of the market product can be compared to that from archived tissue collected in a regulated hunt or documented bycatch for verification of trade records. One of the first efforts to track the individual identity of a whale in trade involved a product from the Japanese market, identified initially as a blue whale, *Balaenoptera musculus*. The mtDNA sequence from this product matched closely with the published sequence of a blue/fin (*B. physalus*) hybrid killed during a scientific whaling program by Iceland. Because mtDNA is maternally inherited, it cannot, by itself, identify a product as a hybrid. Subsequent comparison of variable nuclear DNA introns from tissue archived during the Icelandic whaling program supported the assumption that this product was derived from this hybrid individual (Cipriano and Palumbi, 1999).

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In response to concerns about the continued sale of protected species and the poor control of whale-meat markets, the Government of Norway initiated a program to DNA-profile that all whales taken in its commercial hunt (IWC, 1998). The DNA profiles of each individual whale are stored on an electronic database, forming a "DNA register" of all products intended for the market. If the register is comprehensive or "diagnostic," a match with a market product would confirm the legality of the product (Dizon *et al.*, 2000). A product that did not have a match in the register would be illegal. Further genetic investigation would then be required to determine the species and geographic origin of illegal products. The Governments of Japan has also committed to the development of DNA registers as part of its ongoing programs of scientific whaling and is intended to include the bycatch of baleen whales destined for sale in commercial markets (IWC, 2005b). The effectiveness of the Norwegian DNA register was tested recently with products from North Atlantic common minke whales (*Balaenoptera acutorostrata*) purchased at Norwegian markets. The results demonstrate the matching of the test profiles to the register, confirming the potential power of the DNA registers, but highlighted a number of methodological problems that need to be addressed to ensure successful implementation control of trade (Palsbøll *et al.*, 2006).

p3310 Individual identification of market products can also be a powerful tool for describing market dynamics even in the absence of a AQ52 DNA register or official tissue archive. Dalebout *et al.* (2002) used mtDNA sequences to identify minke whale products sold in Japanese and Korean markets and subsequent DNA profiling to identify replicate products derived from the same individual. Many of these products in both countries were derived from whales taken as unregulated bycatch (discussed later). Individual identification provided information on distribution of products and a minimum "census" of the true number of take in this bycatch. More recently, Baker *et al.* (2007) expanded on this work in the Korean market, using a modified capture–recapture model, based on DNA profiles, to estimate the true number of whales in trade (reflecting the true number killed) over a 5-year period from 1999 to 2003 (discussed later).

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VI. Monitoring of Commercial Markets in Whale, Dolphin and Porpoise Products

p3320 In recognition of historic patterns of over-exploitation, the International Whaling Commission (IWC) voted in 1982 to impose a global moratorium on commercial whaling. Although the moratorium took effect in 1986, whaling never actually stopped. IWC member nations continue to hunt some species of whales for scientific research or for aboriginal and subsistence use. Whales killed for scientific research can be sold legally to domestic consumers and traded to other member nations of the IWC (subject to CITES permits), thereby sustaining a commercial market for meat, skin, blubber, and other whale products. Small cetaceans are also hunted or taken as fisheries bycatch and sold for consumption in many parts of the world (Clapham and Van Waerebeek, 2007). Although the IWC regulates only hunting of large whales, international trade in all cetaceans is subject to CITES. When some species are protected by an international prohibition against hunting or trade but similar species are not, it is crucial to identify the origin of products that are actually sold in retail markets.

In an effort to monitor the sale and trade of cetaceans products, p3330 molecular methods have been used to identify the species and geographic derivation of products sold in two countries with active commercial markets: Japan and the Republic of (South) Korea. Whale meat is widely available in retail markets of both countries despite the international moratorium on commercial whaling (Chan *et al.*, 1995; Mills *et al.*, 1997; Kang and Phipps, 2000). Japan sustains a legal market for whale products through its growing scientific whaling programs in the Southern Hemisphere and the North Pacific Ocean (Gales *et al.*, 2005). South Korea has no program for scientific hunting but reports a substantial fisheries bycatch of cetaceans each year, including minke and other baleen whales (Mills *et al.*, 1997). Products from this unregulated incidental mortality are sold in local markets but their international trade is prohibited by CITES.

Surveys of whale-meat markets conducted, since 1993 in Japan p3340 and 1994 in Korea, have employed both species identification and individual identification to detect the sale of protected species and assess the true take of species in unregulated bycatch or by illegal hunting. As summarized in 2000 (Baker *et al.*, 2000b), surveys of Japanese markets have revealed numerous cases of protected species of large whales including sperm whales (*Physeter macrocephalus*), fin whales, blue/fin whale hybrids, two species of Bryde's whales (*B. edeni and B. brydei*, following the taxonomy of Wada *et al.*, 2003), sei whales (*B. borealis*), humpback whales (*Megaptera novaeangliae*), and gray whales (*Eschrichtius robustus*). With the expansion of the Japanese scientific programs since 2000, however, some formerly protected species are now included in this hunt and regularly available on commercial markets.

Market surveys have also provided information on the diver- p3350 sity of small cetacean products available for sale. In Japan (Endo *et al.*, 2005), a total of 160 "small cetacean" products sold for human consumption in markets from 2000 to 2003 were identified as originating from seven species of the family Delphinidae, one species of beaked whale (*Berardius bairdii*) and one species of porpoise (*Phocoenoides dalli*). In Korea (Baker *et al.*, 2006), a total of 357 whale-meat products, purchased from late 2003 to early 2005, were identified as originating from 15 species of cetaceans: three baleen whales (North Pacific minke, common form Bryde's and humpback), three beaked whales (Stejneger's beaked whale, *Mesoplodon stejnegeri*; Cuvier's beaked whale, *Ziphius cavirostris*; and Blainville's beaked, whale *Mesoplodon densirostris*), seven species of the family Delphinidae (bottlenose dolphin, *Tursiops truncates*; Risso's dolphin, *Grampus griseus*; short-beaked common dolphin, *Delphinus delphis*; Pacific white-sided dolphin, *Lagenorhynchus obliquidens*; false killer whale, *Pseudorca crassidens*; killer whale, *Orcinus orca*; short-finned pilot whale, *Globicephala macrorhynchus*), and two porpoises (harbour porpoise, *Phocoena phocoena*; finless porpoise, *Neophocaena phocaenoides*).

Detailed comparisons of mtDNA sequences and individual identification by DNA profiling have provided information on high levels of unregulated exploitation of minke whales in coastal water of Japan and Korea. The North Pacific minke whale forms at least two stocks with marked differences in frequencies of mtDNA haplotypes(Goto and Pastene, 1997): the "J" stock found in the Sea of Japan/East Sea, and the "O" stock found in the North Pacific to the east of Japan. Although the "O" stock is subject to legal scientific hunting by Japan and is reported to be relatively abundant, the "J" stock was depleted by commercial hunting before 1986 and is considered a "Protection Stock" by the IWC. Using molecular methods and mixed-stock analysis, market surveys from 1993 to 1999 showed a large proportion of products from Japan were derived from the protected "J" stock despite relatively low numbers in official reports of fisheries bycatch (Baker *et al.*, 2000a).

p3370 Surveys of Korean markets have raised similar concerns about exploitation of the "J" stock minke whales. The sale of minke whales reportedly taken as incidental bycatch supports a thriving trade in whale products concentrated in three coastal cities along the southeastern coast of the Korean peninsula: Busan, Ulsan, and Pohang (Kang and Phipps, 2000). As trade in whale products is unregulated, the dynamics of market distribution are not well described (IWC, 2006a). Available information suggests that fishermen negotiate the sale of bycatch informally through a network of perhaps 10 wholesalers operating in these three cities. Whale products are sold in numerous small shops and restaurants in or around Busan, Ulsan, and Pohang, including speciality whale-meat restaurants and large fisheries markets (IWC, 2006). Given the high commercial value of whale and dolphin products (reportedly up to US$100,000 wholesale for an adult minke whale), there is considerable incentive to enhance the potential for bycatch through modified fishing practices, similar to that of traditional "net whaling". Although the Government of South Korea reports relatively large numbers of minke whale as bycatch in its annual progress report to the IWC, market surveys indicate that these records are incomplete, perhaps due to substantial levels of illegal hunting (IWC, 2005a). A capture–recapture analysis of individual market products purchased during market surveys from 1999 to 2003 (discussed earlier, Baker *et al.*, 2007) estimated that the true number of whales entering trade across the 5-year survey period was 827 individuals (CV = 0.24), significantly greater than the officially reported bycatch of 458 whales for this period. Considering results from surveys of both Japanese and Korean markets, the estimated true levels of illegal, unreported, or unregulated exploitation has serious implications for the survival of this genetically distinct coastal population.

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VII. Conclusions

p3380 Molecular methods have great power to detect trade in protected species and to monitor or estimate unregulated or undocumented trade in whales, dolphins, and porpoises. Efforts to improve monitoring and detection of IUU exploitation of cetaceans and control trade in cetacean products would be enhanced greatly by the establishment of diagnostic "DNA registers" (Dizon *et al.*, 2000). The Governments of Japan and Norway have both committed to the development of DNA registers as part of their ongoing programs of scientific or commercial whaling and, in the case of Japan the effort is intended to include the bycatch of baleen whales destined for sale in commercial markets (IWC, 2005b). Korea has made efforts to improve the collection of biological samples from the bycatch of baleen whales (IWC, 2006), although it has not committed to develop a DNA register. No country has yet committed to develop a register for small cetaceans, even though products from directed hunting and bycatch of these species are often destined for commercial markets (Clapham and Waerebeek 2007). p3360

Given the commitment to DNA registers by Japan and Norway, it is puzzling that the governments of both countries oppose implementation of market surveys as a component of any system of observation and monitoring of future whaling. Formal statements by both countries claim that the IWC has no competency in market monitoring (IWC, 2001a, b), although methods for market surveys to estimate bycatch and other human induced mortality have been under discussion at the IWC for several years (IWC, 2003). Assuming a continuation of this political opposition, it is likely the future market surveys will have to follow an "empirical" approach, similar to that advocated for surveys of wild-meat markets (Fa *et al.*, 2004) and including methods of estimation typically used in the molecular ecology of living populations. For countries that regulate hunting or keep official records of bycatch, an empirical approach is likely to require more effort and to yield less precise estimates than combining market surveys with a diagnostic DNA register (IWC, 2006). For countries such as China, Taiwan, Indonesia, and the Philippines, where trade in whale and dolphin products is known or suspected (Barnes,1991; Dolar *et al.*, 1994; Mills *et al.*, 1997) but which keep few records of hunting or bycatch, an empirical approach will be the only option available for monitoring exploitation in the foreseeable future. p3390

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See Also the Following Articles s0980

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Fossil Sites, Noted

R. Ewan Fordyce

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I. Introduction

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Fossil marine mammals—Cetacea, Sirenia, Desmostylia, Pinnipedia and other aquatic carnivores—are known from hundreds of sites worldwide (Fig. 1). Localities span from modern tropics to poles, in both north and south and on all major continents, but with most in northern temperate regions. Usually, sites preserve marine sedimentary rocks, which have been exposed on land through sea level fall and/or uplift, followed by erosion. There are a few records (dredgings) from the deep ocean, and there are some important fresh water sites for secondarily nonmarine species. Fossils give only a general guide to former distributions in ancient oceans. Sites vary from rich localized concentrations at sites a few tens of meters across, to scattered occurrences across many kilometer which become significant at the regional level, and they range in age from Eocene to Pleistocene (Fig. 2). The case studies below, given in sequence from oldest to youngest, span all the major time intervals and oceans.

II. The Role of Geological Processes

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Marine mammal history has been affected by geological changes in oceans and climates over millions (M) of years (Fordyce and Muizon, 2001). These changes ultimately reflect global tectonic processes: continental drift and the rearrangement of land and sea. Continents are now relatively more emergent than for much of the past 50 million years, with less continental shelf and less extensive shallow continental sea than in the past. Most continents preserve coast-parallel strips of ancient marine rock now exposed on land. These may be extensive and a notable source of fossils (e.g., Atlantic Coastal Plain, eastern USA), or limited (e.g., most of Africa). Sometimes extensive shallow epicontinental seas onlapped the continents, as in northern Europe and the Paratethys. Major drops in sea level occurred about 30 million years ago (Ma) and, associated with widespread glaciation and global cooling, since 2 Ma (major fluctuations).

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When the first cetaceans and sirenians appeared, beyond 50 Ma, the extensive shallow Tethys Sea stretched from the Pacific to about the modern Mediterranean. By the end of the Eocene, India had moved northwards to collide with Asia, closing much of the Tethys. More-western remnants of the Tethys, through what is now southern Eurasia, were eliminated in the Miocene, when Africa collided with Eurasia. Later, the Mediterranean dried out completely about 6 Ma, with dramatic consequences for the biota.

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In the south, Australia moved north away from Antarctica opening part of the Southern Ocean by the end of Eocene time (34 Ma). Later, Antarctica and South America separated in the Oligocene (?30, >23 Ma), to open the Drake Passage, allowing west-to-east flow of a newly developed Antarctic Circumpolar Current. This current isolated Antarctica thermally, and probably allowed the Antarctic icecap to expand, global climates to cool, and global oceans to become more heterogeneous. Australia continued to drift north, so that in about Middle Miocene (~15 Ma) it closed the Indopacific seaway between Australia and Asia and restricted equatorial circulation between the Indian and Pacific Oceans. In the middle Pliocene (~3–4 Ma), the Panama Seaway closed, cutting Caribbean–Pacific links. The closure of the Panama Seaway correlates closely with the start of Northern Hemisphere continental glaciation.

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III. A Global Summary of Localities

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Important localities occur in marine sequences around the modern Mediterranean, which is a remnant of the formerly extensive Tethys sea and its now-vanished northeast arm, the Paratethys. Cetaceans, pinnipeds, and sirenians are notable. Italy has many sites of Pliocene to Oligocene age, while the most significant localities along the southern Mediterranean are in the Egyptian Eocene (discussed later). Paratethyan localities to the northeast include some in Austria, Hungary, Slovakia, Croatia, Romania, Ukraine, and several in the Caucasus mountains and borders of the Caspian Sea including Georgia, Azerbaijan, and Kazakstan.

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Eastern North Atlantic cetaceans and pinnipeds have come from Miocene–Pleistocene and, rarely, Eocene-Oligocene sequences bordering the North Sea, in Denmark, northern Germany, Poland, Sweden, Netherlands, Belgium, Britain, and North Sea dredgings. Eocene to Pliocene fossils from the western North Atlantic include